Naturalis Repository

# Legumes

Colin Hughes, Jens J. Ringelberg,
and Anne Bruneau

DOI:
https://doi.org/10.1016/j.cub.2025.03.049

Downloaded from
Naturalis Repository

Article 25fa Dutch Copyright Act (DCA) - End User Rights

This publication is distributed under the terms of Article 25fa of the Dutch Copyright Act (Auteurswet) with consent from the author. Dutch law entitles the maker of a short scientific work funded either wholly or partially by Dutch public funds to make that work publicly available following a reasonable period after the work was first published, provided that reference is made to the source of the first publication of the work.

This publication is distributed under the Naturalis Biodiversity Center 'Taverne implementation' programme. In this programme, research output of Naturalis researchers and collection managers that complies with the legal requirements of Article 25fa of the Dutch Copyright Act is distributed online and free of barriers in the Naturalis institutional repository. Research output is distributed six months after its first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and copyrights owner(s) of this work. Any use of the publication other than authorized under this license or copyright law is prohibited.

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the department of Collection Information know, stating your reasons. In case of a legitimate complaint, Collection Information will make the material inaccessible. Please contact us through email: collectie.informatie@naturalis.nl. We will contact you as soon as possible.

Current Biology
Magazine

CellPress

## Primer

# Legumes

**Colin Hughes**[1,*], **Jens J. Ringelberg**[2], **and Anne Bruneau**[3]

Whatever continent you are on (besides Antarctica), whatever type of vegetation you are in, and however that vegetation has been disturbed and modified by humans, there will very likely be a legume growing nearby. Leguminosae or Fabaceae, commonly known as legumes, with ~22,500 species is the third largest family of flowering plants, after the daisies (Asteraceae) and orchids (Orchidaceae). A central question in legume biology is understanding why the family is so diverse, geographically widespread and abundant, and how legumes came to form significant components of almost all terrestrial ecosystems across the globe. Economically, legumes are also important as major world food crops, and have been so since the dawn of agriculture. The ability to fix atmospheric nitrogen through root nodule symbiosis with bacteria — the hallmark of many legumes — is important in both ecosystem functioning and agriculture, and current research even aims to engineer nodulation in non-legume crops. This combined eco-evolutionary and societal importance means that legumes have occupied a central position in botanical and wider biological research ever since the late 19th century, when Gregor Mendel used the garden pea in his experiments, which famously provided early insights into genetics. In this Primer, we present an overview of the diversity, evolution and ecological and economic importance of legumes across the globe, and discuss the evolution of nodulation, one of the key traits of the family.

## Legumes are everywhere

Legumes are geographically and ecologically cosmopolitan — they grow almost everywhere on the planet. They form ubiquitous and often abundant components of almost all the world's terrestrial ecosystems, from tropical wet and dry forests and savannas, to temperate forests, grasslands, Mediterranean scrub, alpine and tropical-alpine grasslands, and Arctic tundra. Climatically, legumes span a >100-fold range of mean annual rainfall, from 5,000 mm in the hyper-wet tropical forests of the Chocó in South America and the western Ghats in India, to <50 mm on the fringes of the hyper-arid Atacama, Namib and Somali deserts. They also encompass the full spectrum of temperatures and seasonality, from the equator to >70 degrees north in Siberia and Alaska and from sea-level to >5,000 m elevation in the Andes. This wide geographical, ecological and environmental span of legumes reflects the evolution of exceptional diversity of plant functional traits and life history strategies — greater than many other plant families.

Most conspicuously, legumes encompass almost all plant growth forms — from giant, long-lived, 70 m-tall trees and lianas in tropical rain forests to diminutive, short-lived, annual herbs, herbaceous perennials, and twining herbaceous vines in temperate and alpine habitats (Figure 1). Medium-sized, usually deciduous, legume trees are diverse and abundant in seasonally dry tropical forests (Figure 1D,E). Functionally herbaceous geoxyles, with underground lignotubers adapted to survive below ground and re-sprout after fire, characterize many legumes in tropical savannas (Figure 1F). Spiny legume shrubs, often with reduced leaves and photosynthetic stems, are common across several parts of the world's Mediterranean biome (Figure 1G). Low-growing perennial clump-forming rosette or cushion legumes are typical in alpine and tropical-alpine habitats (Figure 1K,L). There is even a freshwater aquatic legume, appropriately named *Neptunia*.

## How did legumes conquer the world?

Legumes have a very rich fossil record. The earliest reliable legume fossils are from early Paleocene 65.3 Ma-old rocks in Colorado, from immediately after the K–Pg bolide impact. Fossil evidence also shows that legumes were already geographically widespread across continents by the Late Paleocene, as well as abundant and diverse in the earliest modern-type rainforests in South America, and legume fossils are ubiquitous in Eocene, Oligocene, and Neogene floras. Fossil evidence suggesting rapid early diversification and spread of the family is in line with molecular phylogenies, which show that the six subfamily lineages are separated by very short branches, indicating rapid initial diversification of the family (Figure 2). Legume crown node age estimates from fossil-constrained phylogenetic analyses span 90–65 Ma, but most of the recently published molecular estimates suggest that legumes started to diversify either just before or close to the K–Pg boundary (Figure 2), thus providing a time frame for diversification encompassing the whole of the Cenozoic.

The emergence of robust and more densely sampled phylogenies (though 50% of legume species still lack DNA sequence data, and a comprehensively sampled global phylogeny needs more work), alongside species geographical occurrence data, are providing potent new insights into questions about the biogeography, tempo and drivers of legume evolutionary diversification. Most legumes are tropical, the family is ancestrally tropical (as seen from the abundance and diversity of fossils in the earliest modern-type tropical rainforests), and legumes show a high level of tropical niche conservatism — most legume lineages never left the tropics. Of those legumes that did move into temperate regions, the vast majority are placed in a single clade (Hologalegina, with ~5,000 species). This transition out of the tropics is associated with a shift from woody to herbaceous growth forms. The small number of species-poor legume tree genera in temperate forests appear to be older, early-diverging relicts from when the tropics encompassed more temperate latitudes in the Eocene. Such lineages may have persisted since then, adapting to life at higher latitudes as the world cooled during the Cenozoic.

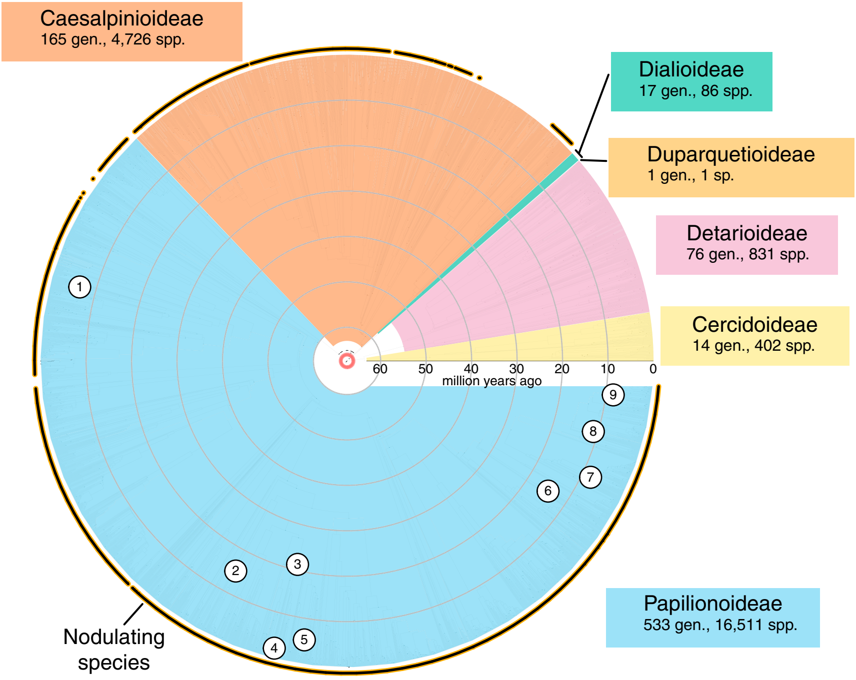
Within the tropics, precipitation has been the main axis of adaptation and phylogenetic turnover. Legume phylogenies generally show high geographical and ecological structure. Thus, while legumes have been able to disperse repeatedly

**Figure 1. Diversity of legume growth forms and habitats.**
(A,B) *Cylicodiscus gabunensis*, canopy-emergent tree to 70 m height in west African tropical rain forest; (C) *Poiretia punctata*, woody liana in tropical rain forest in Peru; (D) *Conzattia multiflora*, deciduous tree in seasonally dry tropical forest, Mexico; (E) *Neltuma kuntzei*, largely aphyllous tree in semi-arid deciduous tropical forest, Bolivia; (F) *Calliandra longipes*, functionally herbaceous geoxyle arising from an underground lignotuber in tropical savanna, Bolivia; (G) *Genista hirsuta*, spiny shrub with reduced leaves, Mediterranean scrub, Portugal; (H) *Lotus maritimus*, dwarf herb in temperate grassland, Switzerland; (I) *Lathyrus ochrus*, twining temperate herbaceous vine with tendrils, Portugal; (J) *Oxytropis halleri*, rosette-forming alpine herb, Switzerland; (K) *Astragalus uniflorus*, tropical-alpine cushion-forming perennial herb, Bolivian Andes: (L) *Lupinus luisanae*, perennial acaulescent herbaceous rosette in tropical-alpine grassland, Colombian Andes. Images: (A) X. van der Burgt, courtesy of Royal Botanic Gardens, Kew; (B) R. Ndonda Makemba; (C–K) C. Hughes; (L) N. Contreras-Ortiz.

between continents and adapt over large tropical rainfall gradients and biomes, only a small fraction (<10%) of divergence events involved trans-oceanic dispersal or an adaptive climatic niche or biome shift. It thus seems clear that dispersal limitation and phylogenetic niche conservatism have strongly shaped legume diversification.

Insights into the tempo of diversification are more elusive, due to uncertainties about the extent of extinction. What is clear, however, is that there were repeated episodes of rapid diversification. These include examples of both recent evolutionary radiations, such as *Lupinus* in the Andes or *Inga* in the neotropical rain forests, whereby hundreds of species rapidly diversified in the Pliocene/Pleistocene, as well as more ancient radiations, such as the initial diversification of the six extant subfamilies in the Paleocene, or the polytomous origin of the pantropical ingoid radiation of >1,700 species in the Oligocene. These phylogenetic patterns suggest that rates of legume diversification have been highly dynamic through time and among clades, more likely following an episodic species turnover model rather than a model involving the steady, gradual accumulation of lineages through time.

The rapid initial divergence of legumes and associated early genome duplications pose challenges for reconstructing the hypothetical ancestral legume genome, geographical area, or morphology. Nevertheless, reconstructions of trait evolution across large clades within legumes show that almost all traits and ecological adaptations have evolved more than once, often numerous times, or have evolved and been subsequently lost. Examples include zygomorphic flowers, spinescence, seed dispersal syndromes, pollen aggregated into polyads, symbiosome-type root nodules, genome duplications, extrafloral nectaries, bi-pinnate leaves, and various growth forms. It is this capacity for repeated re-invention of similar morphologies, functional traits, ecological adaptations, dispersal and pollination syndromes, and plant defense mechanisms that stands out most prominently as a hallmark of the legumes' evolutionary success and their ability to adapt to environmental change.



Current Biology

**Figure 2. Time-calibrated phylogeny of legumes showing numbers of genera and species across the six subfamilies and the phylogenetic distribution of nodulation (outer black line).**
Circles with numbers show genera harbouring important domesticated legume crops: (1) *Arachis*; (2) *Cicer*; (3) *Vicia*; (4) *Pisum*; (5) *Lens*; (6) *Cajanus*; (7) *Glycine*; (8) *Vigna*; (9) *Phaseolus*. The K–Pg boundary is indicated with a red ring close to the root of the phylogeny. Phylogeny based on data from LPWG (2017).

## Phylogeny, classification and genome variability

Given the morphological diversity of legume flowers (Figure 3), it seems, at first sight, improbable that they should be grouped together in a single plant family. The emblematic butterfly-shaped, zygomorphic flower with a showy banner (standard or flag) petal, two lateral wing petals and two keel petals that protect the stamens and gynoecium, which is typical of most species of subfamily Papilionoideae (Figure 3L), is only part of the story. Across the family as a whole, and even within Papilionoideae, legumes show highly labile floral developmental pathways and morphologies in terms of symmetry and the number and arrangements of floral parts (Figure 3), reflecting diverse pollination syndromes that include bee, Lepidoptera, beetle, bat, bird and wind.

Despite this floral heterogeneity, the monophyly of legumes has not been in doubt since the family was first established by de Jussieu in 1789, and it has been amply confirmed in phylogenies. Legumes are united (with some notable exceptions) by two unique diagnostic features. First, the legume fruit itself is usually a single superior carpel with a single locule and the ovules arranged in two alternating rows on a single placenta (Figure 4A,B). Second, the seed coat has an epidermis forming a distinctive palisade with twisted cell walls and hypodermis made up of hourglass-shaped cells, which together constitute the hard impermeable seed coat that often confers prolonged seed dormancy (Figure 4B). The basic legume fruit type has been greatly modified in size, anatomy, ornamentation and palatability to herbivores — traits that promote mechanical (passive or explosive) dehiscence *versus* non-dehiscence, and seed dispersal by water, wind, mammalian herbivores, ants and birds. Compound, once-or twice-divided leaves, although not unique to legumes, are characteristic of the family (Figure 4D). Points of articulation at the base of leaf and leaflet stalks facilitate movement of leaf parts in response to touch (seismonasty — best known in the 'pet plant' *Mimosa*) or light (nyctinasty).

The legume family comprises six lineages that correspond to the recognized subfamilies: Cercidoideae, Detarioideae, Duparquetioideae, Dialioideae, Caesalpinioideae and Papilionoideae (Figure 2). In 2017, this classification replaced the traditional three-subfamily system of Caesalpinioideae, Mimosoideae, and Papilionoideae, which had long been acknowledged as unsatisfactory because of the non-monophyly of Caesalpinioideae. The number of recognized legume genera has been steadily increasing (currently ~806), mainly as improved phylogenies bring genera into line with clades. The number of species, too, continues to rise, with between 50 and 100 new species described each year, and no sign of any slowing down. This is mainly due to new discoveries of globally rare, often threatened, geographically restricted endemics, and also to the recognition of cryptic species and up-ranking of infraspecific variants as species via phylogenetic studies that densely sample species

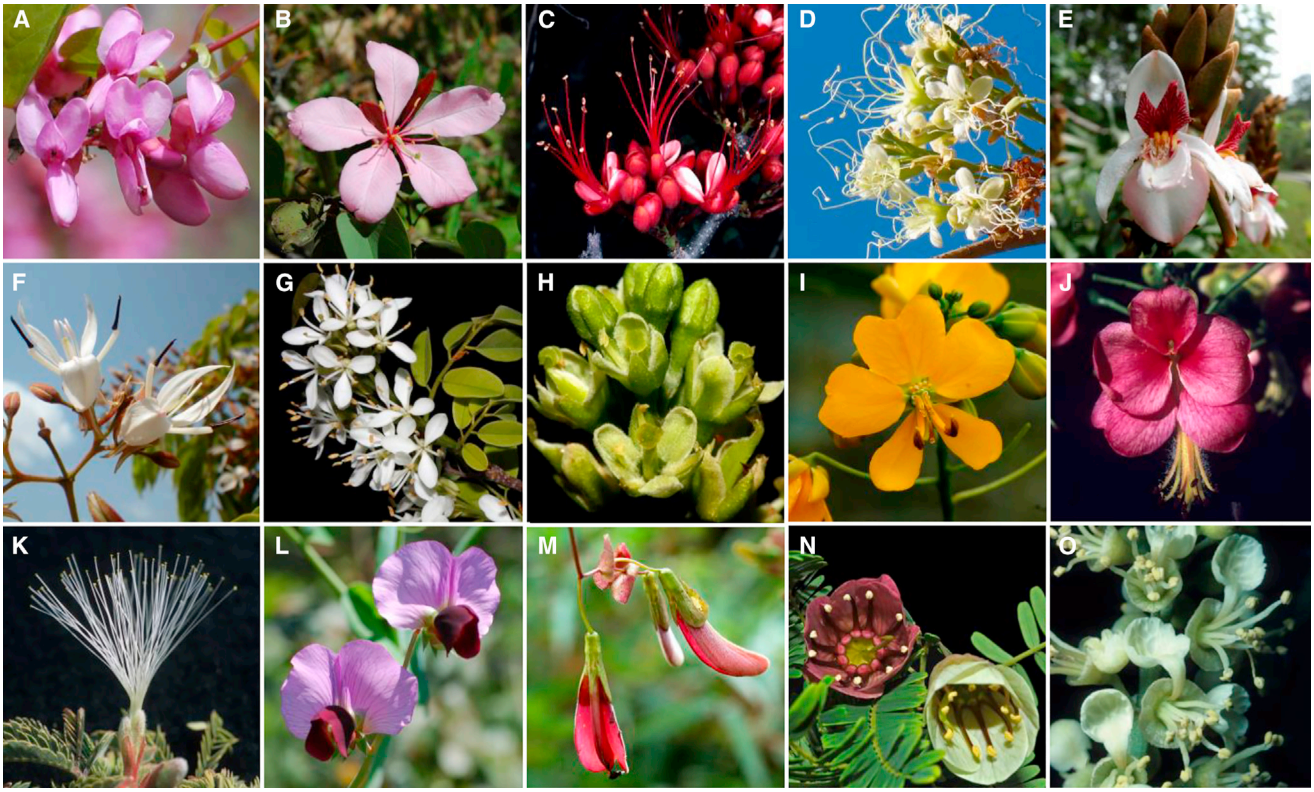


**Figure 3. Diversity of flower morphologies across legume subfamilies.**

(A,B) Cercidoideae; (C,D) Detarioideae; (E) Duparquetioideae; (F,G) Dialioideae; (H–K) Caesalpinioideae; (L–O) Papilionoideae. (A) *Cercis siliquastrum*; (B) *Bauhinia weberbaueri*; (C) *Barnebydendron riedelii*; (D) *Brodriguesia santosii*; (E) *Duparquetia orchidacea*; (F) *Distemonanthus benthamianus*; (G) *Apuleia leiocarpa*; (H) *Gleditsia triacanthos*; (I) *Senna lasseigniana*; (J) *Erythrostemon coccineus*; (K) *Sphinga acatlensis*; (L) *Pisum sativum*; (M) *Amicia lobbiana*; (N) *Cadia purpurea*; (O) *Ateleia herbert-smithii*. Images: (A–C, I–M and O) C. Hughes; (D) G. Lewis; (E) P. Hoekstra; (F) X. van der Burgt, courtesy of Royal Botanic Gardens, Kew; (G,H) D. Cardoso; (N) W. Stuppy.

and intraspecific diversity. Estimates based on models of species accumulation suggest that there are ~2,500 species still to be described, implying total legume diversity of ~25,000 species. The current inventory stands at 22,557 species. These are very unevenly distributed across subfamilies (Figure 2).

Documentation of legume diversity and classification is substantial, including the 2005 illustrated encyclopedia *Legumes of the World* and the *Advances in Legume Systematics* series of 15 volumes published over the last 44 years. This rich source includes a recent classification and illustrated generic conspectus of subfamily Caesalpinioideae in volume 14. In addition, the *Legume Data Portal* (www.legumedata.org) provides further information on legume diversity, including a community-endorsed species checklist.

Recent genome sequencing has rapidly expanded phylogenetic coverage across the legumes. The initial focus was on two model legumes — *Medicago truncatula* and *Lotus japonicus* — plus genomes of the major crop legumes. All of these are taxa of subfamily Papilionoideae, and in 2017, the ten genome sequences used to establish a legume genomics platform were all members of this subfamily. At the time of writing, there are more than 300 publicly available genome assemblies from ~65 genera of legumes, spanning all subfamilies except Duparquetioideae (Papilionoideae: 42 genera/109 species; Caesalpinioideae: 16 genera/29 species; Detarioideae: 3 genera/3 species; Cercidoideae: 3 genera/4 species; Dialioideae: 1 genus/1 species).

Genome sequencing and assembly have revealed extensive genomic variation in legumes, with ploidy levels from 2n=14–112 and 2C-values varying 89-fold. More than 30 whole-genome duplications and one triplication (subtending tribe Genisteae) have been hypothesized across the family. It is clear that several of these duplications occurred during initial evolution of the family, but estimates of the phylogenetic placements and number of early duplications vary from four to six, including the possibility of a pan-legume whole-genome duplication subtending the family as a whole. This complex ancient paleopolyploidy, including probable allopolyploidy, has been characterized as a phylogenomic tangle, resolution of which is likely exacerbated by rapid divergence of the six extant subfamily lineages and by extinction, given that extinct lineages have been inferred as parents in putative ancient allopolyploid events. Additional genome sequencing, including of the sole missing monospecific subfamily Duparquetioideae, will open opportunities for more complete and detailed synteny-informed evaluation of genome duplications and establishment of a fully legume-wide comparative genomics platform. There is little doubt that the expanded genomic substrate afforded by these early legume genome duplications has contributed to subsequent diversification of traits and lineages, but the multiplicity and complexity of the early duplications have limited detailed insights into this so far.

## Domestication of legumes as crops

With their protein-rich seeds and a predilection for open, sunny, often ruderal habitats, a subset of legumes was predisposed to domestication (Figure 2), and many are economically and societally important as major world food crops, second only to cereals (grasses). A diverse set of legume species were domesticated as pulse crops alongside grasses in the key regions where agriculture first arose. These include: adzuki bean (*Vigna angularis*) and soya bean (*Glycine max*) in China and Japan; black gram (*Vigna mungo*), mung bean (*Vigna radiata*) and pigeon pea (*Cajanus cajan*) in India; cow pea (*Vigna unguiculata*) in Africa; garden pea (*Pisum sativum*), faba bean (*Vicia faba*), chickpea (*Cicer arietinum*) and lentil (*Lens culinaris*) in the Fertile Crescent; string, runner and lima beans (*Phaseolus* spp.) (Figures 2 and 4E) in Mesoamerica and the Andes; and peanut (*Arachis hypogaea*) in the Andes. Indeed, a grass–legume domestication partnership underpins traditional and modern agriculture across the globe, with legumes providing an important source of protein and grasses providing carbohydrate for much of the world's human population.

The core legume domestication syndrome includes larger seeds, non-shattering pods, reduced seed dormancy, and very often reduced levels of toxins such as alkaloids in seeds compared with their wild progenitors. Legumes are also important sources of protein for livestock, as evidenced by the global prevalence of legume forage plants with nitrogen-rich leaves and fruits, such as clover (*Trifolium*) and alfalfa (*Medicago*) in temperate pastures and fast-growing legume trees such as *Leucaena* and *Inga* that provide animal fodder and green manure in tropical and subtropical silvo-pastoral and wider agroforestry systems (Figure 4F). Legumes also contribute towards making food production systems more sustainable and carbon-neutral, further emphasizing their global importance in agriculture. On the other side of the coin, their ecological versatility and resilience to disturbance mean that several legumes are also among the world's most pernicious weeds and invasive plants, including Kudzu, *Pueraria montana* in the USA, *Mimosa pigra* in Southeast Asia and Australia, and *Neltuma juliflora* (formerly *Prosopis juliflora*) in East Africa.

**Figure 4. Key features of legumes.**
(A) Typical legume fruits: two *Lupinus* pods each with one valve removed. (B) Typical legume fruits: *Brodriguesia santosii* pods showing seeds with hard, impermeable seed coats. (C) Root nodules of *Lupinus nubigenus* showing the oxygen-carrying, red leghemoglobin protein. (D) The common compound leaf types: pinnate, bipinnate, digitate and trifoliolate. (E) Seeds of the common bean pulse crop, *Phaseolus vulgaris*. (F) Harvesting leaves of *Vachellia nilotica* trees for livestock fodder, Rajasthan, India. Images: (A–C,E,F) C. Hughes; (D) courtesy of R. Wise.

## Nodulation and nitrogen fixation

Nitrogen-fixing root nodule symbiosis (Figure 4C) enables many legumes to access atmospheric nitrogen through symbiosis with diverse soil bacteria known collectively as rhizobia. Nodulation can provide legumes with an extra source of fixed nitrogen. As nitrogen accumulators, legumes are typically characterized as leading a high-nitrogen lifestyle, with high photosynthetic rates in short-lived leaves, and often with nitrogen-rich plant defence compounds and protein-rich leaves and seeds. Nitrogen fixation plays an important role in ecosystem functioning, and provides a sustainable alternative to nitrogen fertilisers in agriculture.

The last two decades have transformed understanding of the molecular genetics, biochemistry and physiology of nodulation. Over 200 core nodulation genes have been identified. There is evidence that the signalling pathways underpinning nodulation were recruited from more ancient pre-existing arbuscular mycorrhizal pathways. Wider diversity and polyphyly of the symbionts involved have been documented, including $\alpha$- and $\beta$-proteobacterial lineages, and data on nodulation ability of genera have expanded.

Although nitrogen fixation and legumes are often thought to go together, not all legumes are able to nodulate, while members of nine other closely related plant families can also nodulate and fix nitrogen. Across the wider nitrogen-fixing angiosperm clade and within legumes, nodulation is phylogenetically unevenly distributed, confined within legumes to Caesalpinioideae and Papilionoideae. Even within these two subfamilies nodulation is far from universal (Figure 2). The phylogenetically scattered distribution across this single angiosperm clade has been known for 30 years, prompting much debate about the evolutionary origins of nodulation.

The difficulties of evolving a functionally and genetically complex novel trait, potentially overcome in part by recruitment of pre-existing mycorrhizal signalling pathways, alongside the clustering of the nine nodulating angiosperm families in a single clade, would seem to point towards a single evolutionary origin of nodulation at the base of the nitrogen-fixing clade, with subsequent secondary loss of nodulation accounting for the numerous non-nodulating lineages. The alternative hypothesis invokes multiple independent evolutionary origins of nodulation (up to 16 across the nitrogen-fixing clade, with six independent gains within legumes, but also ten losses). This hypothesis is suggested by some phylogenetic trait reconstructions and is based on the idea that the ancestor of the nitrogen-fixing clade evolved a precursor, or a stepwise series of precursor transitions, that conferred a genetic predisposition to evolving nodulation only realized in a subset of lineages. However, despite many years of searching, no precursor has been identified. Evidence from genomes that genes essential for nodulation have been independently lost in non-nodulators has also favoured the single-gain and massive evolutionary loss hypothesis.

Whatever the outcome of this complex plant evolutionary biology conundrum, it is striking that both hypotheses infer multiple secondary losses of nodulation, suggesting that evolutionary loss has been prominent, irrespective of how many gains of nodulation there were. Why should an apparently advantageous trait like nodulation be lost? A global evolutionary phenomenon such as evolutionary losses of nodulation across a large number of geographically widespread lineages requires a global explanation. The most convincing explanation is that falling atmospheric $CO_2$ levels during the Cenozoic hampered plant photosynthetic potential to power nodulation, which comes with significant energy costs. This mirrors explanations for the multiple independent evolutionary origins of another complex key plant trait, C4 photosynthesis, which is also thought to have been triggered by falling $CO_2$ during the Cenozoic. In addition, exploitation of nodules by pathogenic bacteria/microbes could have resulted in loss of nodulation in some lineages and driven evolution of the evolutionarily derived symbiosome-type nodule anatomy in other groups. Symbiosomes, typical of core papilionoid and a subset of caesalpinioid legumes, confer a more efficient and intimate symbiosis through tighter compartmentalization of their rhizobial microsymbionts and potentially account for the stable retention of nodulation across these groups compared to lineages with ancestral fixation-thread type nodules.

## Conclusions

In their abundance, geographical ubiquity, diversity, propensity for genome duplication, predominance of morphological and functional homoplasy, and their apparent evolutionary ability to reinvent themselves repeatedly, legumes in many ways exemplify the evolution of angiosperms as a whole. In that sense, legumes are sometimes promoted as a model for flowering plants in ecological and evolutionary studies. Regardless, among all the families of flowering plants, legumes stand out as one of the most spectacular examples of Cenozoic plant evolutionary diversification.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

## FURTHER READING

Bohra, A., Tiwari, A., Kaur, P., Ganie, S.A., Raza, A., Roorkiwal, M., Mir, R.R., Fernie, A.R., Smýkal, P., and Varshney, R.K. (2022). The key to the future lies in the past: Insights from grain legume domestication and improvement should inform future breeding strategies. Plant Cell Physiol. *63*, 1554–1572.

Bruneau, A., de Queiroz, L.P., and Ringelberg, J.J. (2024). Advances in legume systematics 14. Classification of Caesalpinioideae. Part 2: Higher-level classification. PhytoKeys *240*, 1–552.

Fernandes, M.F., Lewis, G.P., Vatanparast, M., Pezzini, F.F., Brown, M.J., de Queiroz, L.P., Cardoso, D., and Pennington, R.T. (2025). Knowledge gaps in legume diversity and distribution and prospects for future research. Brazil. J. Bot. *48*, 8.

Herrera, F., Carvalho, M.R., Wing, S.L., Jaramillo, C., and Herendeen, P.S. (2019). Middle to Late Paleocene Leguminosae fruits and leaves from Colombia. Austr. Syst. Bot. *32*, 385–408.

Jhu, M.Y., and Oldroyd, G.E. (2023). Dancing to a different tune, can we switch from chemical to biological nitrogen fixation for sustainable food security? PLoS Biol. *21*, e3001982.

Koenen, E.J., Ojeda, D.I., Bakker, F.T., Wieringa, J.J., Kidner, C., Hardy, O.J., Pennington, R.T., Herendeen, P.S., Bruneau, A., and Hughes, C.E. (2021). The origin of the legumes is a complex paleopolyploid phylogenomic tangle closely associated with the Cretaceous–Paleogene (K–Pg) mass extinction event. Syst. Biol. *70*, 508–526.

Legume Phylogeny Working Group — LPWG (2017). A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. Taxon *66*, 44–77.

Lewis, G., Schrire, B., Mackinder, B., and Lock, M. (2005). Legumes of the World (London: Royal Botanic Gardens, Kew), p. 577.

Mathesius, U. (2022). Are legumes different? Origins and consequences of evolving nitrogen fixing symbioses. J. Plant Physiol. *276*, 153765.

Ringelberg, J.J., Koenen, E.J., Sauter, B., Aebli, A., Rando, J.G., Iganci, J.R., de Queiroz, L.P., Murphy, D.J., Gaudeul, M., Bruneau, A., *et al*. (2023). Precipitation is the main axis of tropical plant phylogenetic turnover across space and time. Sci. Adv. *9*, eade4954.

Sprent, J.I. (2009). Legume Nodulation: A Global Perspective (Chichester: Wiley-Blackwell).

Stagnari, F., Maggio, A., Galieni, A., and Pisante, M. (2017). Multiple benefits of legumes for agriculture sustainability: An overview. Chem. Biol. Technol. Agric. *4*, 2.

Tucker, S.C. (2003). Floral development in legumes. Plant Physiol. *131*, 911–926.

van Velzen, R., Doyle, J.J., and Geurts, R. (2019). A resurrected scenario: Single gain and massive loss of nitrogen-fixing nodulation. Trends Plant Sci. *24*, 49–57.

Zhao, Y., Zhang, R., Jiang, K.W., Qi, J., Hu, Y., Guo, J., Zhu, R., Zhang, T., Egan, A.N., Yi, T.S., *et al.* (2021). Nuclear phylotranscriptomics and phylogenomics support numerous polyploidization events and hypotheses for the evolution of rhizobial nitrogen-fixing symbiosis in Fabaceae. Mol. Plant *14*, 748–773.

[1]Department of Systematic and Evolutionary Botany, University of Zurich, Zurich, Switzerland. [2]Biodiversity Hotspots, Naturalis Biodiversity Center, Leiden, Netherlands. [3]Institut de Recherche en Biologie Végétale and Département de Sciences Biologiques, Université de Montréal, Montréal, QC, Canada.
*E-mail: colin.hughes@systbot.uzh.ch